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SHORT-TERM VARIATION IN THE BODY WEIGHT OF OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS*: EFFECT OF AVAILABLE FEEDING TIME BY DAY AND NIGHT, TEMPERATURE AND WIND FORCE

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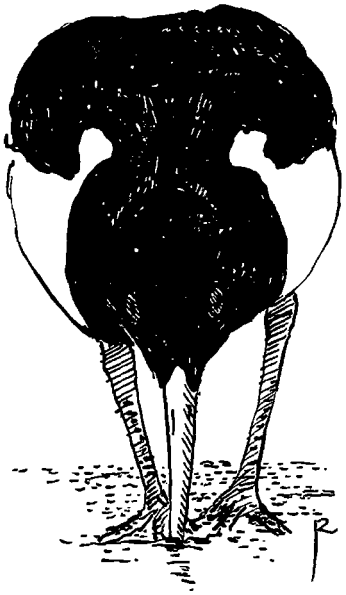
The available feeding time of coastal Oystercatchers varies from day to day due to the effect of wind direction and wind force on the water level. If the birds are not able to feed at all during a day, they lose 30 g, or 6% of their body weight. The body weight increases with the duration of the available feeding time, irrespective whether it is day or night. Oystercatchers continue to feed at night, at least in autumn and winter. Although wind force and wind direction affect the daily duration of the available feeding time, this variation fades away if calculated over a number of days, and therefore does not affect the birds in the long-term. Does the body weight increase, or decrease, with the higher costs of living associated with low temperatures and strong winds? A decrease in body weight with increased cost of living would suggest that the birds are not able to find the extra food required to compensate for the higher maintenance level ('undercompensation'). An increase in body weight, on the other hand, would suggest that the birds in these difficult circumstances eat even more than needed in order to increase their body reserves in cases still worse conditions arrive ('overcompensation'). Unfortunately, the field data are confusing. The weak increase in body weight at low temperatures suggests an overcompensation, but the observed clear decrease in body weight with strong winds suggests an undercompensation. However, the increase of body weight with lower temperature is not large and is possibly due to intervening variables, so it is not clear whether this was an actual overcompensation. The negative effect of wind force on body weight is presumably caused by undercompensation in combination with a decrease in the feeding success.

Key words: Oystercatcher - *Haematopus ostralegus* - body weight - available feeding time - nocturnal feeding - standard operative temperature



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INTRODUCTION

Birds store body energy to survive periods during which they cannot meet their energy requirements. As has been well documented for several small passerines (e.g. Evans 1969, Newton 1969, Lehikoinen 1987), the drain of energy during the nocturnal non-feeding period is so large that each

day body reserves have to be built up again if the birds are to survive the following night. Even more energy has to be stored if the daily food supply is too unpredictable for the bird to be certain that enough food can be found every day (e.g. Jenni & Jenni-Eierman 1987, Rogers 1987, Ekman & Hake 1990, Hurly 1992, Rogers *et al.* 1994, Bednekoff & Krebs 1995, Witter *et al.* 1995).

Like these other birds, Oystercatchers build up strategic nutrient stores to survive periods during which they cannot meet their daily requirements (Dare 1977, Goss-Custard *et al.* 1982, Johnson 1985, Zwarts *et al.* 1996d), but body weight would also be expected to vary from day to day as a result of the daily variation in the time for which the tidal feeding areas are exposed. The birds may even have no access to the low water feeding areas when gales increase the water level so much that the tidal flats do not expose at all. Forced periods of fasting that last many days occur in frost periods when the mudflats are frozen or covered by ice.

This paper compares the variation in body weight with the variation in the exposure time over the days before birds were weighed. The prediction is that the body weight should decrease during periods when the exposure time is short, unless the birds can compensate by increasing their intake rate (Swennen *et al.* 1989), or by extending their feeding time on the higher shore during ebb and flood tides or in the fields at high tide. Since Oystercatchers usually feed on the lower shore, the daily variation in the exposure time of this part of the shore must be ascertained, which can be done most conveniently with a tidal gauge. These data have been continuously registered for many years in many places, enabling the long-term probability that a feeding area will be exposed during a given low water period at certain times to be easily calculated. When such data are available, the exposure times may also be calculated separately for day and night, providing an opportunity to test whether the light conditions during the exposure time affect the feeding behaviour of Oystercatchers.

Besides exposure time, the body weight may be affected by the costs of living. The daily consumption of captive Oystercatchers is 36 g and is independent of temperature above an air temperature of 10°C (Kersten & Piersma 1987; see also Zwarts *et al.* 1996c). In order to compensate for their enhanced heat loss at lower temperatures, the birds have to increase their daily food consumption by 5% for every degree the temperature is below thermoneutrality (Kersten & Piersma 1987). Indeed, the daily consumption may increase even more than 5% because the birds increase their body weight as the temperature drops (Kersten & Piersma 1987, Goede 1993). However, Kersten & Piersma (1987) and Goede (1993) were able to give their captive birds food *ad libitum*, but free-living birds may not be equally able to get so much food in extreme winter conditions. That they might be able to do so is suggested by the work of Swann & Etheridge (1989) who found the highest body weights at the lowest winter temperatures in Oystercatchers and some other wader species wintering in Scotland. If waders are indeed generally able to increase their body weight in harsh circumstances, they would be expected also to be able to survive cold spells. This is not true, however, since many Oystercatchers starve to death at low temperatures (Swennen & Duiven 1983, Stock *et al.* 1987, Hulscher 1990, Zwarts *et al.* 1996d). These apparent conflicting results make it worthwhile to analyse the relationship between body weight and temperature.

Wind force may also have an indirect effect on body weight because the thermoregulation requirements of waders living on windy shores is more effected by wind chill than by temperature alone (Wiersma & Piersma 1994). In this paper, we apply the formulae of Wiersma & Piersma (1994), who estimated the heat loss of a Knot *Calidris canutus* on mudflat and bare salt marsh, and use the measurements of wind force, temperature and global solar radiation to estimate the standard operative temperatures, a measure of chill or environmental temperature.

The paper addresses four questions: (1) how predictable is the duration of the exposure time of the low water feeding area, (2) does the body

weight vary with the duration of the exposure time, (3) to what degree do Oystercatchers use the nocturnal exposure times to feed, and (4) do the body weights increase, or decrease, with low temperatures and strong winds?

METHODS

The analysis is based upon a sample of adult and subadult Oystercatchers captured at high water roosts along the Frisian coast, Dutch Wadden Sea. The majority were caught in one area, locally known as the 'Paesenserpolder' (53°21'N, 6°06'E). The analysis was performed on 2140 birds captured on 70 days between 1977 and 1986. At least seven birds were caught at one time either with mistnets at night or cannon nets by day. The analysis of the variation in winter weight was restricted to the period December-February, the three months during which the body weight, although fluctuating, remains at a roughly similar level (Zwarts *et al.* 1996d). In total, 462 birds captured on 18 days between 1977 and 1982 were processed in these three months.

Oystercatchers lose weight on the roost, especially over the first four hours due to defecation. Hence, a correction was made for the time the birds had already spent on the high water roost by adjusting weights to their value at 4 h in the roost. Weight was subtracted if the roosting period had been 4 h or less and added if the elapsed non-feeding time had been more than 4 h (Fig. 3 in Zwarts *et al.* 1996f). A correction was also made for body size differences with all weights being standardized to an Oystercatcher with a wing length of 263.5 mm (Zwarts *et al.* 1996e).

The fluctuations in body weight were tested against three weather variables. We took the 24 h averages of temperature (°C), wind force (m s^{-1}) and global solar radiation (W m^{-2}), measured at the nearby weather stations of the Free University of Amsterdam at Schiermonnikoog or of Rijkswaterstaat at Lauwersoog, both situated some km from the study area. In order to relate body weight to available feeding time, we had to know in which part of the tidal zone the birds fed. Since Oystercatchers feed on cockle and mussel beds which are predominantly found at, and below, mean sea level we defined the available low water feeding period as the length of time for which the water level was below 0 cm relative to mean sea level. These data were taken from the tidal gauge of Rijkswaterstaat at Lauwersoog. The water levels at Lauwersoog were compared to the measurements of a tidal gauge placed in the centre of our study site for one year. The incoming and receding tides reached the level of 0 cm relative to mean sea level in our study site 23 min later than in Lauwersoog. The time lag did not vary during the incoming tide, but was less constant during the receding tide. This variation was found to be related to wind direction and force, so the exposure time for the mudflats in our study area could be predicted accurately with the aid of the continuous water level measurements at Lauwersoog combined with data on wind direction and wind force. To calculate separately the potential feeding time by day or by night, the low water periods were divided up relative to civil twilight.

Average temperature and wind force were calculated for time spans of different length: on the day of capture; on day of capture and the day before; on the day of capture and the two days before, and so on up to seven days before capture. We did the same for the duration of one to eight low water feeding periods preceding the capture. Experience showed that the correlations were highest when average body weight was plotted against temperature and wind force on the day of the capture or, in the case of the exposure period, the last low water period preceding the capture. The effects of these three variables on the body weight decreased, and even disappeared, if a greater number of days or exposure periods preceding capture were included in calculating the average. Therefore, we will only show the relationships between body weight and the weather variables on the day of capture and between body weight and the last exposure time before capture.

To investigate to what degree birds continued to feed at night, we used a hide on a high tower to

count the feeding and non-feeding Oystercatchers on 3 ha of mudflat. The counting area formed a part of the Nes area (see Fig. 1 in Zwarts *et al.* 1996g). The counts were performed several times per hour over the entire exposure time: seven low water periods fell completely in daylight but, on five occasions, sunset occurred at dead low water. An infra-red binocular was used to continue the counts after dark. During the seven daylight periods, the density of feeding Oystercatchers after low water was 70-90% relative to the counts made before dead low water. The night-day ratio given in the paper is the ratio of the density counts done with the infra-red binocular in the dark and the ordinary binoculars in daylight, multiplied by 0.8 to correct for the decrease in the numbers over the low water period that was observed in the daylight emersion periods.

All statistical analyses were performed with SPSS, a standard statistical package (Norušis 1990).

RESULTS

Variation in available feeding time

The relationship between tidal height and average emersion time for our study area could be perfectly described with a third degree polynomial (Fig. 1B). Comparison of Figs. 1A and 1B shows that the tidal flats at 20 cm below mean sea level were exposed for 5 h per low water period, this being equivalent to 40% per 24 h, since there are 1.93 low water periods per day. The first Oystercatchers left the high water roost when the water level was 20 cm above mean sea level and the last birds returned to the roost at the same water level. However, the majority of the birds only fed when the tidal flats below mean sea level were exposed (Fig. 1C). When the water level was between 0 and 20 cm relative to mean sea level, they usually gathered in pre-roosting and post-roosting flocks on the mudflats.

For these reasons, we used a water level of 0 cm relative to mean sea level to define when the feeding areas were exposed or immersed. On this criterion, the feeding areas exploited by Oystercatchers were exposed, on average, for 5.5 h on spring tides and for 6 h on neap tides (Fig. 1B). This still involved a systematic overestimation of the actual time which individual Oystercatchers spent on the low water feeding area. Blomert *et al.* (1983) registered the behaviour of colour-banded Oystercatchers in the study area in late summer and autumn from the moment they left the high water roost until they returned. They found that the birds were present on the feeding area for only 79.4% (SE = 3.3%, n = 9) of the time during which the water level was below 0 cm, which was 66 min less than the average exposure time of 338 min. The same difference (69 min) was found if the actual feeding time was calculated on the basis of the times of arrival of birds on the low water feeding areas, which was noted in 17 individuals, and the times of departure from the feeding area, which was known for 13 individuals (Blomert *et al.* 1983). As all birds did not arrive and depart at the same time, we conclude that the individual feeding times at low water were 4.5-5 h, whereas birds were present on the feeding areas for 5.5-6 h.

Although there was not much difference between spring and neap tide in the emersion time of mudflats situated at mean sea level (Fig. 1B), there was a large daily variation in the exposure time, depending on the wind force and wind direction. In the Wadden Sea, a gale from the northwest causes an elevation of the water level of 1 m or more, whereas a similar wind from the southeast has the reverse effect (Fig. 2). Strong winds are rare in summer, and more common in late autumn and early winter, so that the variation in the emersion time is most pronounced in the period October-January (Fig. 3A). Due to the prevailing westerly winds during these months, the average exposure time is relatively short (10.3-10.6 h) in October-January. In contrast the exposure times are long (11.5-12.1 h) in February-May. Were waders in NW. Europe not to feed at low water at night, the average available exposure time would decrease from 10.5 to 4 h per day in mid-winter and from 11 to 8.5 h in May-July. The daily varia-

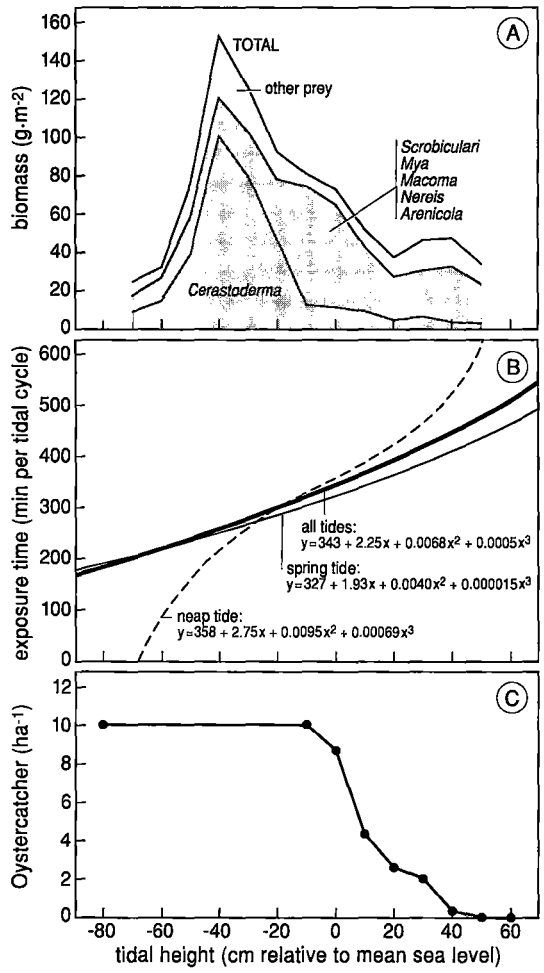

Fig. 1. (A) The average biomass (g ash-free dry weight m^{-2}) in August of the macrozoobenthos as a function of the elevation of the tidal flat relative to mean sea level, divided between Cockles *Cerastoderma edule*, other bivalves (*Macoma balthica*, *Mya arenaria*, *Scrobicularia plana*), worms (*Nereis diversicolor*, *Arenicola marina*) and other benthic prey not taken by Oystercatchers (from Zwarts 1988; averages for six sampling sites along the mainland coast of the Dutch Wadden Sea during eleven years, 1976-1986). (B) The exposure time in the eastern part of the Dutch Wadden Sea as a function of the elevation (from Zwarts 1988; based upon continuous water level measurements in Lauwersoog over ten years). (C) Oystercatcher density as a function of the water level (from Zwarts unpubl.; averages of 316 bird counts in July-October 1976 in a site along the Groningen mainland coast (Dutch Wadden Sea), made from the receding to the incoming tide in 51 plots which were situated between the high and low water line.

tion in exposure time in daylight is, of course, much larger than the emersion times over 24 h, especially in winter (Fig. 3B).

Figure 3 shows that the low water feeding areas do not always provide the same feeding opportunities. Instead of the average exposure time of 11 h in late autumn and early winter, the feeding area is exposed for less than 4 h on 5% of the days, and is even not exposed at all on 1% of winter days. Of more importance, however, is to establish how often such extreme restrictions occur on consecutive days. Starvation experiments show that even small waders do not die when they are unable to feed for just one day (e.g. Davidson 1983) and Oystercatchers easily survive a starvation period of several days in summer and more than a week in winter (Hulscher 1990, Hulscher *et al.* 1996, Zwarts *et al.* 1996d). Therefore, we calculated how often mudflats situated at mean sea level are exposed for a certain time during one day, during two successive days, and so on, up to seven days (Fig. 4A). It is clear that calculated over a time span of several days, very short exposure times do not occur. In other words, wind may reduce exposure time for one day, but the effect is never so long-lasting that it prevents waders from feeding on the tidal flats for several days. But, if waders were not able to feed at low water at night, the probability that they would hardly be able to feed for several days in succession in winter would be about ten times as large (Fig. 4B).

In order to investigate the effect of exposure time on body weight, we used the average weight (Fig. 3 in Zwarts *et al.* 1996d) as the base line, and calculated for each day the average deviation from these monthly means. Body weights appeared to be relatively high when the exposure times before the capture were long, and to be below the expected average when the available feeding time was short. These results are not shown be-

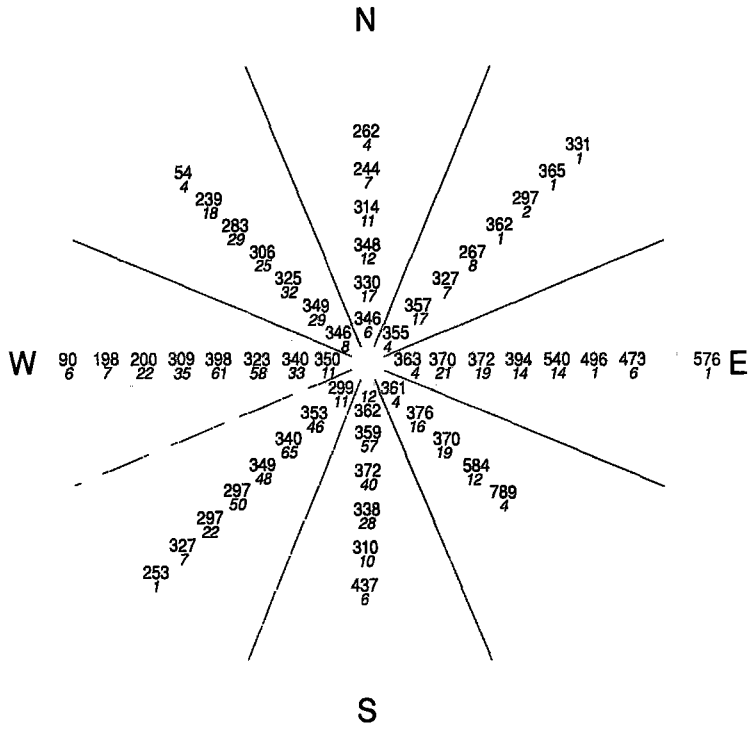

Fig. 2. Exposure time of a tidal flat situated at mean sea level as a function of wind direction (i.e. eight points on the compass) and wind force (m s^{-1} on 24 h before low water) in the study area using the tidal gauge of Rijkswaterstaat at Lauwersoog, 1977-1991. The top number gives the average exposure time in minutes per low water period and the bottom number the frequency of occurrence (‰).

cause, as Fig. 3A already revealed, the variation in exposure time was rather limited in summer. Since extreme short and long exposure times only occurred in winter, we will examine the effect of exposure time on body weight in a next section only for the winter.

We also investigated the deviation from the average monthly body weights against the exposure time during the daylight hours in the last and two preceding low water periods. Were the birds not to feed at night, or were their intake rate to be much lower at night than by day, the duration of the low water period during daylight would be more critical than the duration of the exposure time per 24 h. This night effect was analysed in different ways, but did not increase the amount of variance explained. This suggests that it does not matter to Oystercatcher whether the feeding areas are exposed by day or by night.

The importance of nocturnal feeding

Do Oystercatchers indeed feed at night? Observations at night with infra-red binoculars and light amplifiers showed that they did. However, since we did not measure intake rate, the nocturnal consumption could not be quantified. Intake rate could be estimated, however, since consumption during the daylight hours has been determined by Blomert *et al.* (1983). They studied an individually marked population of Oystercatchers in our study area between July and November 1979. The intake rate during daylight feeding was measured in birds which, according to their body measurements, could be distinguished as ♂♂

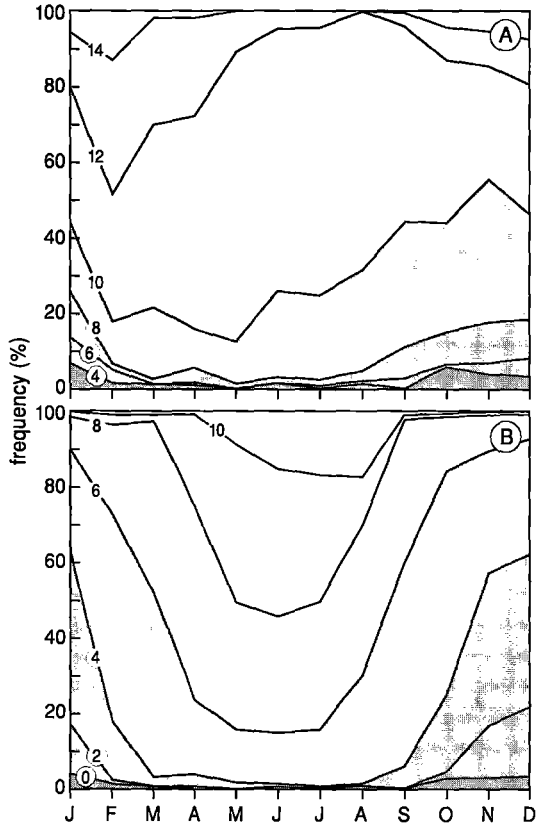

Fig. 3. (A) The relative frequency with which tidal flats at mean sea level are exposed for 4, 6, 8, 10, 12 or 14 h a day during the course of the year. (B) As upper panel, but referring to the exposure time in daylight only (time between civil twilight). Data from Rijkswaterstaat (tidal gauge Lauwersoog, 1977-1987).

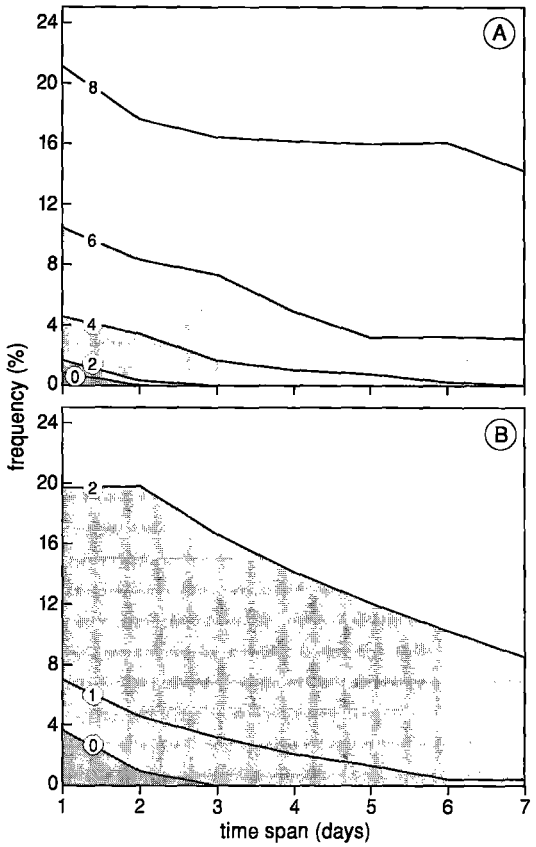

Fig. 4. (A) The relative frequency with which tidal flats at mean sea level are exposed for an average of 0, 2, 4, 6 and 8 h a day in December-January, calculated over a time span of 1, 2, .. 7 days. (B) As upper panel, but for exposure times in daylight only (time between civil twilights). Same data as Fig. 3.

and ♀♀ (Fig. 5A). The total time the birds spent feeding at low tide was known (Fig. 5B), so the daily consumption in daylight could be calculated.

As in other years, Oystercatchers kept that year their body weight constant from July till October and increased their weight in November (Zwarts *et al.* 1996d). Moreover, the air temperature did not fall below thermoneutrality, so we assume that the birds needed each month a similar amount of food, this being 36 g ash-free dry flesh per day. Due to the weight difference between the sexes, we further assumed that the daily consumption was 1 g higher for ♀♀ than for ♂♂.

The intake rate during feeding decreased during late summer and autumn, due to the declining prey condition (Zwarts 1991) and because their benthic prey, *Macoma balthica* and *Scrobicularia plana*, increased their burying depth (Zwarts & Wanink 1993). Note that the intake rate of the ♀♀ was much higher than of the ♂♂, being 27% higher in August, 54% in September, and 20% higher in October (Fig. 5A). ♂♂ compensated for their relatively low intake rate by feeding for longer than ♀♀ (Fig. 5B).

The required daily food consumption could be

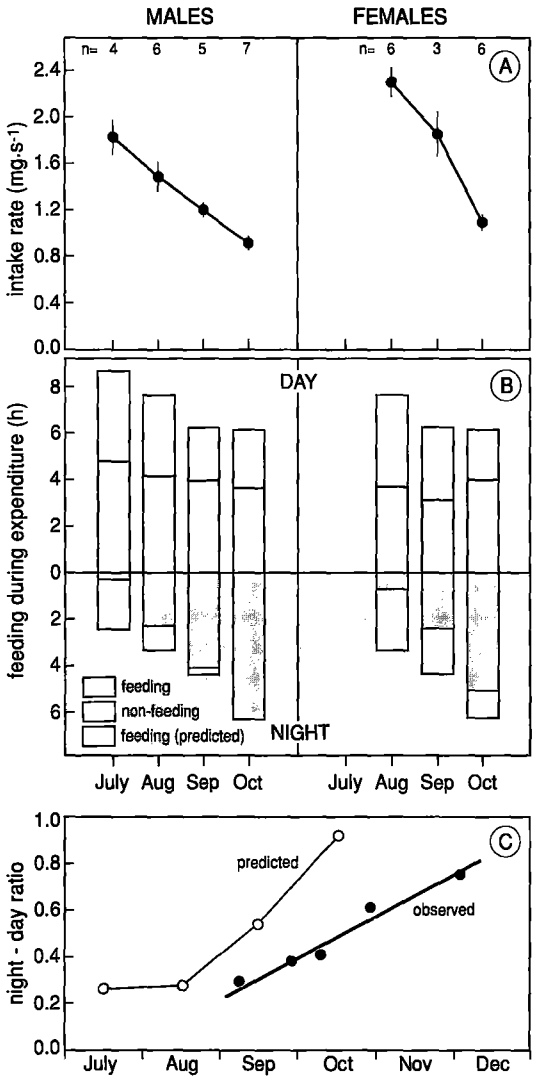

Fig. 5. (A) Average intake rate during feeding (mg s^{-1} ± *SE*) of male and female Oystercatcher feeding on a diet of *Macoma balthica*, *Scrobicularia plana* and *Mytilus edulis*. All data from Blomert *et al.* (1983), who recorded the feeding behaviour of individually marked Oystercatchers along the Frisian coast; *n* = number of low water periods; *SE* refers to daily variation. (B) Exposure time by day and by night, and the duration of the feeding time by day (based on observations) and the predicted nocturnal feeding time, assuming that the average daily consumption is 36 g and that the intake rate by night equals the intake rate by day in the same month. The nocturnal feeding time in October is overestimated since an unknown part of the food is obtained by day at high tide in the fields. The Oystercatchers never fed in the fields in July-September. (C) Percentage of Oystercatchers that remained to feed at night compared to daylight (Zwarts unpubl.; for details see methods), compared to the predicted feeding time, derived from panel B.

obtained by feeding in daylight alone in July and August, but not later on. Assuming that the intake rates at night were equal to those by day in the same months (Fig. 5A), we calculated for how long the birds would have to feed at night to meet their energy requirements (Fig. 5B). The prediction that, in contrast to late summer, the birds had to feed for many hours over the nocturnal low water periods in autumn could be checked by direct observations during the same period (Fig. 5C). In fact, fewer birds appeared to feed at night than predicted. This was not surprising because we did not taken into account the fact that the birds began in October to feed in fields at high tide by day. Thus, the predicted nocturnal feeding time was overestimated. On the other hand, the predicted duration of the feeding time on the mudflats at night was based upon the assumption that the intake rate at night was equal to the intake by day. Several studies have shown, however, that intake rate might be 40-50% lower (Heppleston 1971, Zwarts & Drent 1981, Sutherland 1982a, Goss-Custard & Durell 1987), although others found no difference (Hulscher 1976, Leopold *et al.* 1989, Kersten & Visser 1996b, K.-M. Exo pers. comm.). Figure 5 shows, however, that Oystercatchers would not have been able to balance the daily food requirement if their intake rate at night was less than by day, at least in ♂♂ in August and September when they did not feed in the fields.

The seasonal increase in nocturnal feeding was partly due to the shorter day-light period (Fig. 5B), but mainly to the decline in the intake rate (Fig. 5A). The decrease in intake rate was larger than the average seasonal trend (Fig. 17 in Zwarts *et al.* 1996b), so one might expect that the

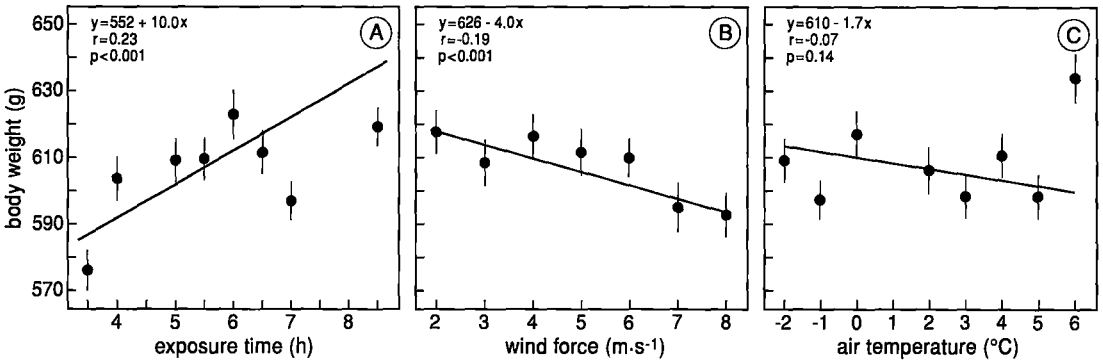

Fig. 6. Average standardized body weight of Oystercatchers in winter as a function of (A) the exposure time in the low water period before capture, (B) the wind force during the 24 h before capture and (C) the average daily temperature. The regressions were performed on the 462 individual birds, but since the individual weight variations were so large, we have plotted means ± *SE*.

shift to nocturnal feeding may often be less pronounced than was observed in 1979 (Fig. 5C). Indeed, three years later, Bruggemann (1985) found in the same area no seasonal variation in the numbers of Oystercatcher feeding by day and by night, with Oystercatchers continuing to feed at night even in summer. The food supply was very poor in that year (Zwarts *et al.* 1996g), so probably the birds had always to feed at night to compensate for the low intake rate.

In conclusion, Oystercatcher probably preferred to feed at low tide by day, but if this was not sufficient to meet their energy requirements, they also fed at low tide by night.

Variation in body weight in winter

In our study area, Oystercatchers weighed 610 g, on average, during the winter but the average weight varied from day to day between 580 and 660 g. A part of this variation could be explained by the length of the exposure time over the low water period before the birds were captured (Fig. 6A). A strong wind had a negative effect on the body weight (Fig. 6B), while temperature had a similar, but less pronounced, effect (Fig. 6C). Unfortunately, most birds were captured during rather mild winter conditions, and hardly any during frost. Moreover, the three independent variables were related. The correlation was -0.37 for exposure time *versus* wind force, r = -0.36 for exposure time *versus* temperature and r = +0.32 for wind force *versus* temperature. Wind was negatively correlated with exposure time since strong winds usually blow from the west, which causes an elevation of the water level, and thus a decrease of the exposure time (Fig. 2). Strong winds from the west are in winter also associated with mild weather. This made it less easy to interpret the results. A multiple regression analysis revealed that the effect of exposure time remained largely present ($SE = 2.20, p < 0.001$), while the effect of wind force was substantially reduced, although it was still significant ($SE = 0.52, p < 0.01$):

body weight (g) = 572 + 8.45 × *exposure time* (h) + 0.96 × *temperature* (°C) - 2.80 × *wind force* (m s^{-1}).

The weakly significant, negative relationship between body weight and temperature in the bivariate plot (Fig. 6C), actually became positive in the multiple regression equation, but its contribution to the explained variance was too low to be significant ($SE = 1.20, p = 0.42$). The equation did not change much when body weight was regressed against exposure time and wind force alone:

body weight (g) = 576 + 7.97 × *exposure time* - 2.62 × *wind force*,

with $p = 0.0002$ and $SE = 2.12$ for exposure time, and $p = 0.018$ and $SE = 0.50$ for wind force.

An alternative way to investigate the effect of the weather variables, with the influence of exposure time taken into account, was to calculate the deviations from the simple regression of body weight against exposure time and plot these residuals against wind force and temperature. Whereas the effect of temperature was not significantly different from zero ($y = -0.7 + 0.2x$), the wind effect remained significant ($y = 11.9 - 4.5x$), where y represented the residual (g) and x the exposure time (h).

In conclusion, the body weight increased by about 8 g for each hour increase in length of the exposure time, decreased by about 15 g if there was a strong wind, whereas temperature had a negligible effect.

DISCUSSION

Can Oystercatchers feed on the high shore?

In comparison to other waders, Oystercatchers spend a long time on the high water roost. They arrive at the roost on the incoming tide when, for instance, Redshank *Tringa totanus* and Dunlin *Calidris alpina* are still feeding at the tide edge. Oystercatchers also remain on the roost on the receding tide when other wader species have already begun to feed on the first exposed areas (Goss-Custard *et al.* 1977, Hale 1980, Tubbs & Tubbs 1980, Dann 1987, Zwarts *et al.* 1990, Ketzenberg & Exo 1994, Hötker 1995). A possible explanation for this is that large waders, such as Oystercatcher and Curlew *Numenius arquata*, are able to balance their energy demands by feeding during a shorter period than small waders since the intake rate relative to the metabolic requirements increases with body weight (Zwarts *et al.* 1990). However, this does not explain why Oystercatchers restrict their feeding period to the hours around low water. The reason for this is that the food supply on the high shore is usually too poor to provide Oystercatchers with an intake rate that is high enough to make it worthwhile feeding there (Sutherland 1982b, Ens *et al.* 1996). Cockles *Cerastoderma edule* and Mussels *Mytilus edulis* are the major prey for Oystercatchers. Most mussel beds are found below mean sea level and are thus only available as feeding area during < 4-7 hours per tidal cycle (e.g. Zwarts & Drent 1981, Goss-Custard & Durell 1987). The Cockle only reaches its highest biomass densities below mean sea level, and the same is true, although to a lesser degree, for the alternative prey, the bivalves *Macoma balthica*, *Mya arenaria* and *Scrobicularia plana* and the worms *Nereis diversicolor* and *Arenicola marina* (Beukema 1976, Wolff & de Wolf 1977, Meire 1996; see also Fig. 1A).

Exposure time and variation in body weight

Oystercatchers are able to keep their body weight constant in thermoneutral conditions, at an air temperature of at least 10°C (Kersten & Piersma 1987, Zwarts *et al.* 1996c), if they consume 36 g dry flesh per day (Hulscher 1982, Kersten & Piersma 1987, Goede 1993, Zwarts *et al.* 1996b). We also know that wild Oystercatchers lose about 30 g a day if they do not feed at all (Kersten & Piersma 1987, Kersten & Visser 1996b). Thus daily change in body weight (W_c, g fresh weight) is a function of food consumption (C, g ash-free dry flesh):

$$W_c = -30 + 0.83C$$

Oystercatchers can spend 1.93 low water periods per day on the feeding grounds. The average exposure time in our study area is 654 min day^{-1}, or 338 min per low water period, which, as shown above, overestimates by just over 1 h the time that individual Oystercatchers actually spend on the feeding areas. This means that the average estimated time on the feeding area is 519 min day^{-1}, or 269 min per low water period. Assuming that an average Oystercatcher does indeed feed for so long, its intake rate must average 1.15 mg dry flesh s^{-1} during this period, non-feeding intervals included. If this average intake rate, for feeding and non-feeding intervals combined, does not vary with the duration of the exposure time, the

daily change in body weight (W_c, g fresh weight) is a function of duration of the feeding time (F, h):

$$W_c = -30 + 3.5F$$

In other words, the body weight would decrease, or increase, by 3.5 g per day, for each hour the available feeding time is reduced, or increased with the average of 8.65 h. As shown in the multiple regression equations above, the slope of body weight on exposure time was 8 g h^{-1} (SE = 2), more than twice as large as the maximum expected (Fig. 6A).

It is surprising that the actual effect of exposure time on body weight is greater than the expected maximum of 3.5 g h^{-1}. Indeed, we might have expected the observed values to be lower, not higher, because Oystercatchers may compensate for the variation in exposure time. First, Oystercatchers may response to short exposure times by feeding more in the field at high tide (Daan & Koene 1981), as indeed happened in our study area (Zwarts unpubl.). Second, Oystercatchers do feed on the high shore, which they normally ignore when, due to gales, the low shore remains covered at low tide (Zwarts unpubl.). Third, Oystercatchers spend a lower proportion of the time feeding when the exposure time is long (Fig. 6 in Zwarts *et al.* 1996c). Fourth, Oystercatchers seem able to feed at a higher rate when the exposure time is short (Swennen *et al.* 1989). These behavioural responses would appear to make the birds less dependent on the length of the exposure time, so the question remains as to how to explain the observed relationship between body weight and exposure time.

The intake rate of Oystercatchers during feeding has been measured in many studies and appears to vary between 1 and 3 mg s^{-1} feeding (Zwarts *et al.* 1996a & b). Hence, Oystercatchers which attain a high intake rate do not need to feed for 8.5 h a day; this is another reason to expect in many situations no relationship between daily consumption, and thus change in body weight, and exposure time. However, Kersten & Visser (1996a) showed that the gut processing rate is only 0.66 mg s^{-1} and thus much lower than the rate at which food is usually ingested. This implies that Oystercatchers feeding at, for instance, a rate of 2.2 mg s^{-1} cannot continue to feed at that rate beyond 2 h, because of a digestive bottleneck (Fig. 1 in Zwarts *et al.* 1996c). The discrepancy between gut processing rate and feeding rate also explains why Oystercatchers are less active on long exposure times (Fig. 6 in Zwarts *et al.* 1996c). The major implication of the low maximum gut processing rate is that birds have to spend a long time on the feeding area to achieve the daily consumption needed, irrespective of whether the intake rate during feeding is 1 or 3 mg s^{-1}. This makes the duration of the exposure time over the low water feeding area a potentially more important predictor of the daily consumption then might otherwise be expected. It also explains why Oystercatchers cannot restrict their feeding time to low water period by day only, except in mid-summer. Moreover, the intake rate of Oystercatchers that feed on the upper shore during gales appears to be extremely low (Ens *et al.* 1996, Zwarts unpubl.) and provides little towards the total daily consumption. The intake rate in the fields are also rather low (Heppleston 1971, Hosper 1978, Zwarts & Blomert 1996, summarized in Zwarts *et al.* 1996b).

In conclusion, the daily consumption primarily depends on the duration of the exposure time, even though the birds seem to be less active when the exposure time is long and the intake rate during feeding may be enhanced when the available feeding time is reduced. However, the low gut processing rate forces the birds to pause during feeding due to the digestive bottleneck and this makes it important for the birds to be able to spread out the feeding bouts over an extended period. Moreover, the intake rate in the fields at high tide and on the upper shore are apparently not sufficient to compensate for the low consumption on the usual low water feeding areas when these are exposed for only short periods. The strong effect of exposure time on body weight suggests that the average intake rate is lower, and not higher, on short low water periods.

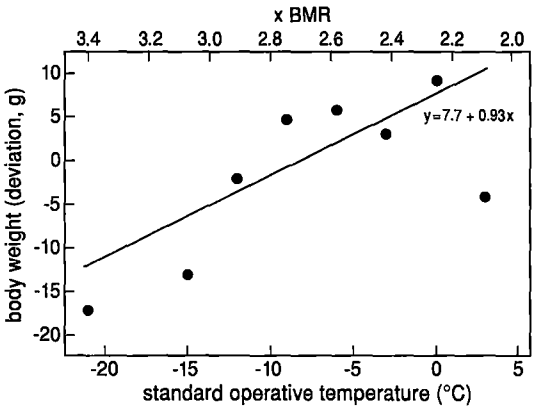

Fig. 7. Body weight of adult Oystercatchers as a function of standard operative temperature and the existence metabolism, given as ratio relative to basal metabolic rate (Wiersma & Piersma 1994; further explanation see text). To correct for the effect of exposure time, the deviations from the regression line 'body weight *versus* exposure time' (Fig. 6A) were used to be plotted against the standard operative temperature.

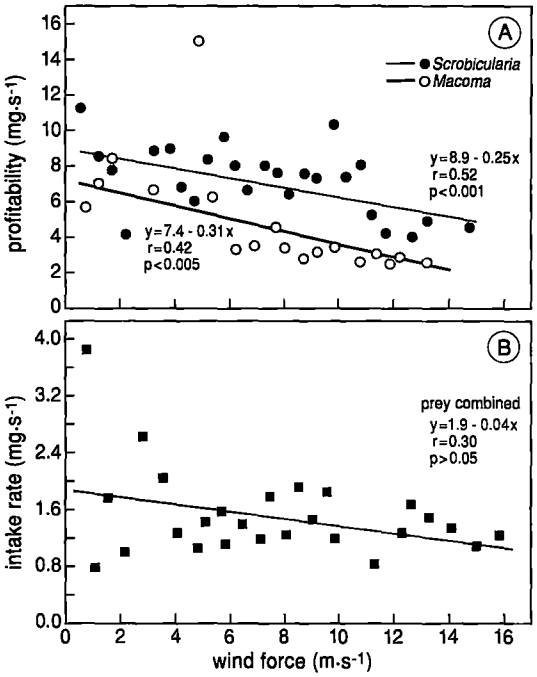

Fig. 8. (A) The profitability (mg s^{-1} handling) of two bivalve species as a function of wind force; prey weight and handling time have been measured in 430 *Macoma balthica* and 199 *Scrobicularia plana*. (B) Intake rate (mg s^{-1} feeding) of Oystercatchers feeding on a mixed diet of *Macoma*, *Scrobicularia* and Mussels (from: Blomert *et al.* 1983).

Weather conditions in winter and variation in body weight

Based on work on heat loss in Knot, Wiersma & Piersma (1994) estimated the heat loss (H) to be a function of temperature (T, °C), wind speed (W, m s^{-1}) and global solar radiation (R) according to the equation:

$$H = (0.045 + 0.00809 \times 1.15W^{0.75}) \times (41 - T) - 0.0008R.$$

During the 18 days of capture in winter, the average daily wind force varied between 2 and 8 m s^{-1}, equivalent to 2-4 Beaufort. The average daily temperature on the same days varied between -2 and 6°C. Within these ranges, we would expect that the effect of temperature on heat loss to be twice as large as that of wind force. However, when we plotted for the days of capture the calculated H against the three weather variables, H appears to be strongly related to wind force (r = +0.93), hardly at all to radiation (r = +0.21) and not at all to temperature (r = -0.05). Thus, it is not surprising that, in our data, there was no relationship between body weight and temperature, whereas there was a significant negative effect of wind force on body weight (Fig. 6). As a consequence, the body weight decreases when standard operative temperature goes down from +3 to -21°C and the costs of the existence metabolism increases by more than 60% (Fig. 7). This suggests that Oystercatchers wintering in the Wadden Sea are at the energetic fringe, since they have to catabolize a part of their energy reserves as soon as the energy demand increases.

Wind force, however, not only causes an increase in the costs of living but also negatively affects the feeding circumstances. First, the average exposure time decreases with wind force. This ef-

fect has been taken into account since Fig. 7 plots body weights corrected for the duration of the exposure time. Second, the average intake rate may decrease with wind force, because the downshore and best areas are not much exposed. Third, as found by Blomert *et al.* (1983), it takes Oystercatchers in windy circumstances more time to handle prey such as *Macoma* and *Scrobicularia*, which caused the profitability of these prey significantly to decrease with wind force (Fig. 8A). As a consequence, wind force has also a negative effect on the intake rate (Fig. 8B), a phenomenon also observed in two other waders species, viz. Grey Plover *Pluvialis squatarola* (Pienkowski 1981, Dugan *et al.* 1981) and Redshank (Davidson 1983). Hence, the decrease in body weight at windy days may be directly affected by the reduced food consumption.

There are thus two explanations for the lower body weight in strong winds: heat loss and lower intake rate. It is not possible with the field data collected so far to indicate which of the two is the more important. Detailed observations on intake rate in combination with a large-scale catching program are needed to solve this question. A decrease in body weight during spells of inclement weather had not been expected, unless feeding was impossible. First, captive Oystercatchers increased their body weight at low temperatures (Kersten & Piersma 1987, Goede 1993), as was also observed by Swann & Etheridge (1989) in free-living Oystercatchers, Redshank and Knot. Also Pienkowski *et al.* (1979) referred to unpublished data showing that winter weights of Dunlins were lower in mild winter conditions. In Oystercatchers, the same trend was found when birds from different wintering areas were compared (Zwarts *et al.* 1996d). Finally, an increase in body weight as an immediate reaction on cold weather has commonly been observed in many passerines (e.g. Newton 1972, Ekman & Hake 1990, Peach *et al.* 1992, Rogers *et al.* 1994, Pilastro *et al.* 1995). On the other hand, a drain of winter reserves in harsh winter weather has been documented for six wader species: Bar-tailed Godwit *Limosa lapponica* (Evans & Smith 1975), Grey Plover (Dugan *et al.* 1981), Golden Plover *Pluvialis apricaria* (Davidson 1981), Redshank (Davidson 1983), Dunlin (Davidson 1981, Steltloperringgroep FFF 1983) and Curlew (Steltloperringgroep FFF 1983).

The tentative conclusion of this paper is that Oystercatchers and other waders are not exceptions compared to other bird species and also attempt to increase their body weight at low standard operative temperatures. However, wintering waders in the temperate zone are often at the energetic fringe. They are buffeted on the exposed tidal flats by gales which make feeding less successful, while in frost the available feeding areas are covered by ice. How close waders wintering in the temperate zone are to the fringe, is suggested by the increase in mortality that occurs as soon as the temperatures goes down (e.g. Jukema & Hulscher 1988, Meininger *et al.* 1991, Camphuysen *et al.* 1996, Goss-Custard *et al.* 1996, Zwarts *et al.* 1996g).

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SAMENVATTING

Windrichting en -kracht beïnvloeden de getijbeweging en daarmee de beschikbare foerageertijd van wadvogels (Fig. 2). Als Scholeksters een hele dag niet kunnen voedselzoeken verliezen ze 30 g, of 6%, van hun lichaamsgewicht. De dagelijkse gewichtsverandering hangt samen met de duur van de beschikbare foerageertijd (Fig. 6A), en daarbij maakt het niet uit of het dag of nacht is. Scholeksters foerageren 's nachts gewoon door, zeker in de herfst en de winter (Fig. 5). Hoewel windrichting en -kracht de duur van de dagelijkse foerageertijd sterk beïnvloeden, valt deze variatie geheel weg als de variatie in droogligtijd wordt berekend over meerdere dagen (Fig. 4). Aangezien Scholeksters genoeg lichaamsreserves opslaan om minstens enkele dagen zonder eten te kunnen, heeft de variatie in droogligtijd geen lange termijn effect op de vogels. Een krachtige wind heeft wel een negatief effect op het lichaamsgewicht (Fig. 6B). Hierbij spelen waarschijnlijk twee effecten door elkaar heen. Ten eerste, maakt een harde wind het moeilijker om voedsel te vinden (Fig. 8). Ten tweede, nemen de thermoregulatiekosten toe waardoor het leven duurder wordt (Fig. 7).

In het laboratorium, en ook in een Schots estuarium, werd gevonden dat de vogels zwaarder werden bij lagere temperaturen. Onze veldgegevens daarentegen suggereren dat Scholeksters het onder barre winterse omstandigheden niet kunnen bolwerken en hun reservestoffen moeten aanspreken.